GENETICS AND TERRESTRIAL MOLLUSC CONSERVATION

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Genetic analysis of populations provides information on the genetic structuring of populations and their breeding systems. Much of this type of information is presently not readily available for most invertebrates. Terrestrial molluscs are well known amongst geneticists for providing models of evolutionary phenomena. Both traditional and modern genetic analyses have been done on many species and these provide ideas which may be applicable to other molluscs as well as invertebrates in general. The genetic analysis of species in the native slug family Cystopeltidae is given as an example of the use of genetic analysis in the determination of structuring and breeding system. Comparisons are made to other terrestrial molluscs and the implications for their conservation discussed. □*Genetics, population structuring, terrestrial mollusca, Cystopeltidae, slugs, captive breeding, Australia.*

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Genetic diversity is the basis of biodiversity and the loss of genetic diversity means that a species or populations has a reduced ability to track long term environmental changes (Frankel, 1970; Frankel & Soulé, 1981). One of the difficulties in trying to maintain genetic diversity is defining the level (e.g. population or species) at which genetic management should take place or how it could be done. There is no standard theory or method of assessing the desirable 'amount' of genetic variability a species or population 'needs' for long-term survival. The use of genetic data to decide on a 'quantitative basis' whether populations contain 'sufficient' genetic diversity to remain viable is still in its infancy despite great advances in techniques. Most ideas of genetic conservation have been based on a mixture of empirical data and on general genetic models which are yet to show predictive ability. However as more examples become available a more rational basis for biodiversity conservation should emerge.

The conservation of genetic diversity requires firstly an estimation of the extent of genetic variation within a species and within and between populations. Genetic analyses of a population can provide a reasonable method of determining not only the extent of population differences but also levels of inbreeding or selfing which may not be detected by direct observation or laboratory experiments. This is particularly true for the vast majority of invertebrates with little hope of breeding under controlled conditions to determine breeding system. Measures of the amount of gene flow between populations and species are also possible, showing the extent of their isolation as well as testing validity of species status.

Terrestrial molluscs, as with most invertebrates, have been largely neglected in the species conservation debate. Apart from a few notable examples such as *Partula* (Johnson et al., 1986; Murray et al., 1988; 1991) and *Cerion* (Gould et al., 1974; Gould & Woodruff, 1978; Woodruff, 1989) genetic studies of terrestrial molluscs have been predominantly on the non-tropical northern hemisphere species. The bulk of these tend to concentrate on the highly polymorphic species such as *Cepaea* (Cain, 1983 & references there in; Murray, 1975). Considerable information is available for many european and north American species, and while representing a small proportion of all terrestrial species, do provide a general understanding of the dynamics of terrestrial mollusc populations. These studies show high levels of genetic differentiation between populations as well as a variety of breeding systems. In some instances different populations of the same species exhibited different breeding systems, i.e. outcrossing vs self-fertilization (Selander & Ochman, 1983; Foltz et al., 1982, Anderson & McCracken, 1986). Research on tropical species tend to be freshwater species involved in parasite transmission such as *Biomphalaria* (Mulvey et al., 1988; Vrijenhoek & Graven, 1992).

MEASURING GENETIC DIFFERENCES

Various genetic analyses can be used to characterise the differences between populations and species. The average observed heterozygosity, H_0

and the proportion of polymorphic loci, *P* are straightforward measures of the amount of genetic variability that can be used as general evaluation of a population. Populations in which H_0 is zero are generally thought to be, in the case of molluscs, the result of self-fertilization. Self-fertilization takes place when sperm fertilizes an egg from the same individual. Low or zero values for *P* are also indicative of self-fertilizing populations. Other explanations for low values of H_0 and *P* could be the result of population bottleneck, founder effects or strong selection forces (Frankel & Soulé, 1981). However these measures don't take into account differences at specific loci and so different populations of the same species with the same H_0 and *P* could still differ significantly in the alleles present. Other commonly considered measures are the so called *F*-statistics devised by Wright (1951) describe the arrangement of genetic variation in a subdivided population with two, F_{IS} and F_{ST} being the most useful. F_{IS} gives a measure of the non-random association of alleles within a population and can be used to infer the type of breeding system. Positive values indicate heterozygote deficiency, negative values an excess. F_{ST} is a measure of the genetic differentiation between populations. The average frequency of alleles found in only one population, $\bar{p}(1)$ (Slatkin & Barton, 1989) can give an indication of actual allelic differences between populations. Where gene flow is restricted then the frequencies attained by these 'private' alleles will be high in comparison with populations where flow is greater. These alleles are useful in observing the direction of gene flow in small populations. The so called genetic distances, such as Nei's *D* and Rogers *R* are also routinely used to express the differences between populations and species. These two measures take into account the amount of allelic frequency differences and fixed differences between populations. The larger the value the more distant the populations or species.

AUSTRALIAN TERRESTRIAL MOLLUSCAN FAUNA

Inadequate genetic work has been carried out on the Australian mollusc fauna. Genetic analysis has been used to differentiate species, such as *Bothriembryon* in Western Australia (Hill et al., 1983), however little has been done on the genetic structuring of mollusc populations. The dynamic nature of many Australian ecosystems, particularly those of the south east, with habitat mosaics caused by fires, would presuppose that many species of molluscs would show considerable genetic structuring. In other areas high biodiversity of species is reflected in genetic structuring of populations. Woodruff & Solem (1990) found in the Kimberley region that the extensive radiation of camaenid snail species was accompanied by significant levels of genetic differentiation within species. Much more work has been done on freshwater species. For example Stoddart (1983) examined genetic variation in *Thiara balonnensis* while Ponder & Clark (1988) and Ponder (1994) have used allozymes for both species discrimination and examination of population structuring in freshwater snails. Some work has been done on introduced species. For example Johnson (1988) examined the founder effects and geographic variation in the introduced terrestrial snail *Theba pisana* in Western Australia. However, if conclusions on preserving genetic diversity are to be sound, genetic structuring in the common or widespread species also needs to be evaluated.

THE CYSTOPELTIDAE

Cystopeltidae is a family of slugs restricted to eastern Australia and found in a wide range of forest habitats (Smith & Kershaw, 1979). They appear to feed primarily on bark-dwelling micro algae and bacteria abundant in eucalypt forests. The family appears to be composed of mostly allopatric species which are discernible on morphological characters (Daniell, 1992). The analyses of various genetic measures of allozymes show that, as found with other terrestrial molluscs, species and populations show significant structuring (Table 1). Amongst the *Cystopelta* species mean H_0 for populations ranged from 0.042 to 0.179 and *P* ranged from 0.16 to 0.36 values which are comparable with other terrestrial slugs (Foltz et al., 1982). A more detailed analyses of cystopeltid populations (Daniell, 1992) found that within species some populations exhibited very little or no variability and very low levels of heterozygosity. Within one species most populations had low to very low numbers of polymorphic loci. These results are indicative of selfing as is typical among many populations of slug species found in europe (Foltz et al., 1984) although localized inbreeding as a result of colonisation by a few individuals or a massive population crash followed by a prolonged bottleneck can not be discounted. One difficulty with these types of measure is the effect

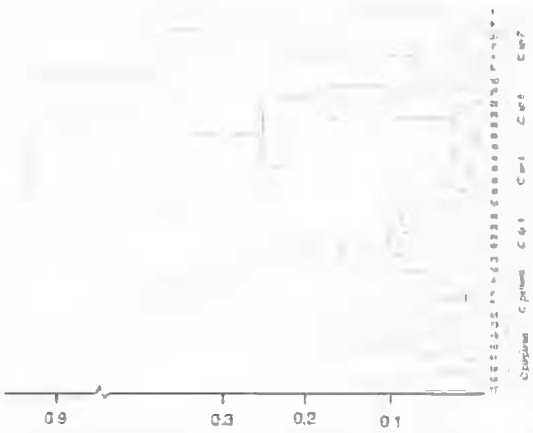

FIG. 1. UPGMA (unweighted pair group method) of Nei's genetic distances for *Cystopelta* species. Numbers refer to populations. Population 12 is of unknown taxonomic status.

of sampling area size. Sampling errors either being sampling 'populations' which are in fact panmictic or sampling over a larger area, which may encompass a number of discrete populations. In either case this will result in an incorrect interpretation of the genetic structure of the species. To over come these types of errors a reasonable sampling regime requires an understanding of the organism's biology.

The F_{IS} values in cystopeltid species ranged from 0.05 to 0.55. These indicate heterozygote deficiency which may be the result of localised inbreeding or selfing. Despite these results most populations appear to be outerossing with most values of F_{IS} being non-significantly different from zero. F_{ST} values between populations ranged from 0.192 to 0.661 and indicate that there is considerable subpopulation heterogeneity. This is not an unexpected outcome as most terrestrial molluscs have poor dispersal ability and so can exhibit extensive population structuring even on a relatively small scale. Ochman et al. (1987) found mean F_{ST} values for both *Cepaea nemoralis* and *C. hortensis* of approximately 0.20 between demes. Stiven (1989) found mean values of F_{ST} of 0.065 and 0.116 for two species of *Mesomphix* in north America. The Populations of the introduced species *Theba pisana,* in Australia, had F_{ST} values as great as 0.301 (Johnson, 1988). Selander & Whittam (1983) found extensive differentiation within populations of *Helix aspersa* introduced into California.

Geographic distances between populations in these studies varied from adjacent populations to those separated by as much as 25km, with high levels of genetic differentiation being largely independent of the actual distances. As with F_{IS} values, F_{ST} results for the cystopeltids show a large variation between species. The variability of values is indicative of the chance factors affecting which alleles exist and in what frequency in each population. Founder effects, drift, selection along with breeding system all play a part in shaping the genetic make-up of a population. There also appears to be no significant correlation between the level of genetic differentiation and geographic distance between populations (Daniell, 1992). As suggested by Kemperman & Degenaars (1992) sampling regime may have a big influence in the genetic structure found. They found that genetic difference within subspecies of *Albinaria* were detectable at distances of less than 200m. In the case of cystopeltids a detailed examination of a single locality, (*C. purpurea* population 17) samples from three sites 140m apart, had a F_{ST} value of 0.015, a magnitude less than those found for the species as a whole. This suggests, at least for this species, that deme size could be quite large. Therefore sampling for any genetic analysis should encompass detailed ecological parameters so that subsequent results can have some conservation significance.

Genetic distances (Fig. 1) show a similar picture to the other measures with no consistency of

TABLE 1. Species, number of subpopulations, average population size, average heterozygosity H_0, proportion of polymorphic loci *P*, mean *FIS*, mean *FST*.

SPECIES	No. of Subpops	Av. N	*H0*	*P*	*FIS*	*FST*
Cystopelta bicolor	1	2	0	0	0	0
C. petterdi	3	18.3	0.08	0.21	0.07	0.47
C. purpurea	7	36	0.18	0.32	0.32	0.37
C. purpurea PO	3	29.6	0.16	0.36	0.39	0.015
C. sp. 1	6	21.6	0.03	0.21	0.55	0.66
C. sp. 2	5	18.8	0.07	0.16	0.05	0.58
C. sp. 3	5	12.6	0.18	0.32	0.16	0.19

genetic distances between populations within species. This could be expected, because as demonstrated by F_{ST} values, structuring of the populations is not uniform, reflecting the different evolutionary histories of each population. A detailed examination of *Albinaria* species (Kemperman & Degenaars, 1992) showed a similar situation, where populations of different species and subspecies showed marked variation in genetic similarity. Clearly not all populations are equal and this suggests that populations are a more useful unit of conservation than species. The other significant feature is the usefulness in highlighting the possibility of previously undescribed species, particularly in widespread and variable organisms. What does the genetic data tell us about terrestrial mollusc populations? Firstly, it is unlikely that a single species can be used as general model for a family. Variability between cystopeltid species for all genetic measures used was high, with no consistent trend. Secondly detailed analyses of populations (Daniell, 1992) indicates, as found from other studies, that populations themselves can differ significantly from the species average for genetic measures. In some cases one population could exhibit the characteristics of a selfing population (H_o & P of zero) and another could be polymorphic and largely outcrossing.

It is yet to be established that populations with high levels of genetic variability are more 'successful' than those with less. While the general case is that variability is needed for evolutionary processes to takes place, and little or no variability in a population is a long-term disadvantage (Frankel & Soulé, 1981) very high levels of variability have not been shown to be of highest benefit. There is strong evidence that levels of heterozygosity can have an influence on various fitness characters. In marine bivalves *Mytilus* spp. heterozygosity has been correlated with increased growth rates and adult survival (Koehn & Gaffney, 1984) and in *Placopecten magellanicus* heterozygosity at one locus was associated with increased mobility (Volckaert & Zouros, 1989). For both these examples the mechanism appears to involve the reduced metabolic requirements of heterozygous individuals, although this may more significant when the organism is in a more stressful environment (Skibinisski & Roderick, 1989). Triggs & Sherley (1993) correctly point out that the amount of variation within populations is as important as between. Where a species consists of a number of populations each exhibiting a high level of genetic variability then any single one could contain a significant representation of the alleles in that species. In contrast species which have low variability within populations then more than one populations would be needed to maintain genetic variability within the species.

The study of co-adapted genes in land snails has concentrated on the more obvious features such as shell pattern and colour (Cain, 1983; Cook, 1986; Goodhart, 1987) and body colour (Cowie, 1990). Cryptic species or those which are less subjected to visual selection and so little in the way of 'obvious' characters are available to study. In the case of minute snail species, such as the punctids and charopids whose movements are restricted by size and the risk of desiccation, they appear to be restricted to microhabitats and therefore possibly adapted to small isolated populations. These populations have probably undergone severe bottleneck events and so through inbreeding or even selfing may exhibit low levels of heterozygosity and polymorphic loci. As yet no genetic analyses has been done on the minute Australian species but Cook & Lace (1993) looked at, among other things, genetic structuring in the small helicoid *Heterostoma paupercula* (Gastropoda: Helicidae). These snails live under rocks on sparsely vegetated oceanic islands and the F_{ST} value was found to be 0.435, not an unexpected result. Heterozygosity was also less than expected. However, other large and apparently more mobile groups such as the cystopeltids can also exhibit high F_{ST} values. This may reflect a common feature of terrestrial mollusc populations; high levels of genetic differentiation. This in itself may be a product of the low mobility and dispersal capabilities of terrestrial molluscs in general.

GENETIC MANAGEMENT OF INVERTEBRATE POPULATIONS

At its most fundamental genetics provides a measure of the genetic diversity and distribution in species and populations. The genetic structuring of a population reflects its evolutionary history. The high levels of genetic differentiation observed in molluscs mean that some caution should be applied to their genetic management. As such, any modification of genetic structure through captive breeding or translocation is fraught with uncertainty. For example the mixing of two unrecognised species or genetically distinct populations could result in disruption of particular gene combinations and reducing fit-

ness. Any program of captive breeding will lead to some selection for the ability to thrive in captivity which may be detrimental to any future re-releases into the 'wild'. Species that do well in captivity may be 'pre-adapted' to the situation as a result of the changes that led to it becoming endangered and may not provide a general model for all species. As can be observed in the case of *Partula* not all species, even if closely related, are thriving in captivity (Tonge & Bloxam, 1991). The idea of preserving a 'single' species would also present difficulties particularly in the case where many genetically distinct populations can be observed. Which populations should then be preserved? It has been suggested that the greater the genetic distance between populations the higher the preservation priority (Triggs & Sherley, 1993). This would presuppose that one could predict which population and hence which combination of alleles is likely to be the most successful. This approach also ignores the role of rare or restricted alleles in future evolution in populations and species. Crozier (1992) proposes that populations be the most appropriate unit for preservation, and genetic distance data be used as a basis of population ranking, the rationale being that not all populations within a species are 'equal'.

The detailed analyses of genetic structuring should be done *before* species become endangered or at risk. The current mode of genetic evaluation is *after* a species is recognized to be in a difficult position, by which time genetic disruption may have already occurred. This is made a less reliable approach owing to the generally poor state of the basic biology of a species and difficulties in devising a sampling protocol. A more complete understanding of non endangered species may give an insight into the 'normal' genetic structure to populations, however it is unlikely with the current level of understanding of population dynamics that simple models will be available to 'predict' the outcome of disrupting the genetic structure of a population though captive breeding or translocation. The genetic protocol produced for the Moorean *Partula* species (Tonge & Bloxam, 1991) sets a bench mark for other such programs. As a general model for breeding programs however it is somewhat limited since the *Partula* species had been thoroughly studied well before extinction in the wild became inevitable (Clarke & Murray, 1969). Populations were well enough known to be sure that samples were from panmictic populations. This is in contrast with the majority of species where the level of knowledge of their basic biology, let alone their genetics, is poor. General principles need to be established to provide guideline for the management of invertebrate species. It is clear from the difficulties with husbandry of *Partula* species (Tonge & Bloxam, 1991) that captive breeding is a last resort. The role of genetic factors in the decline of a species is in most cases not the most important factor. Where genetics does contribute is in clarifying the dynamics of populations especially where other methods of observation are unlikely to provide answers, such as estimating breeding systems and gene flow. It is also useful in taxonomic studies, particularly where morphology is highly variable or in the case of minute species difficult work with because of size and difficulty in finding specimens. In the case of *Cystopelta* a large sized, widespread and common organism was found to have many more species than previously described. As new techniques become available it will be possible to more rapidly evaluate genetic structuring and breeding system.

The situation is urgent for many terrestrial molluscs. The currently estimated number of species, around 30,000, is probably a gross underestimation. Genetic analysis has shown that in most species significant genetic differentiation exists even in those which are common and widespread. This is probably indicative of the levels of speciation that are occurring in particular in tropical species. It would be a first step if captive breeding and population re- establishment of species into previously known ranges to test the applicability of techniques. It would also be of some benefit that institutions such as zoos could become involved in the display and breeding of local molluscs species both to foster some local interest and also to develop expertise well before it is needed.

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